

Dangerously few liaisons: a review of mate-finding Allee effects

Joanna Gascoigne · Ludek Berec · Stephen Gregory ·
Franck Courchamp

Received: 2 July 2008 / Accepted: 28 January 2009 / Published online: 1 May 2009
© The Society of Population Ecology and Springer 2009

Abstract In this paper, we review mate-finding Allee effects from ecological and evolutionary points of view. We define ‘mate-finding’ as mate searching in mobile animals, and also as the meeting of gametes for sessile animals and plants (pollination). We consider related issues such as mate quality and choice, sperm limitation and physiological stimulation of reproduction by conspecifics, as well as discussing the role of demographic stochasticity in generating mate-finding Allee effects. We consider the role of component Allee effects due to mate-finding in generating demographic Allee effects (at the population level). Compelling evidence for demographic Allee effects due to mate-finding (as well as via other mechanisms) is still limited, due to difficulties in censusing rare populations or a failure to identify underlying mechanisms, but also because of fitness trade-offs, population spatial structure and metapopulation dynamics, and because the strength of component Allee effects may vary in time and space. Mate-finding Allee effects act on individual fitness and are thus susceptible to change via natural selection. We believe it is useful to distinguish two routes by which evolution can act to mitigate mate-finding Allee effects. The first is evolution of characteristics such as calls, pheromones, hermaphroditism, etc.

which make mate-finding more efficient at low density, thus eliminating the Allee effect. Such adaptations are very abundant in the natural world, and may have arisen to avoid Allee effects, although other hypotheses are also possible. The second route is to avoid low density via adaptations such as permanent or periodic aggregation. In this case, the Allee effect is still present, but its effects are avoided. These two strategies may have different consequences in a world where many populations are being artificially reduced to low density: in the first case, population growth rate can be maintained, while in the second case, the mechanism to avoid Allee effects has been destroyed. It is therefore in these latter populations that we predict the greatest evidence for mate-finding Allee effects and associated demographic consequences. This idea is supported by the existing empirical evidence for demographic Allee effects. Given a strong effect that mate-finding appears to have on individual fitness, we support the continuing quest to find connections between component mate-finding Allee effects (individual reproductive fitness) and the demographic consequences. There are many reasons why such studies are difficult, but it is important, particularly given the increasing number of populations and species of conservation concern, that the ecological community understands more about how widespread demographic Allee effects really are, and why.

J. Gascoigne (✉)
School of Ocean Sciences, University of Wales Bangor,
Menai Bridge LL59 5ES, UK
e-mail: j.gascoigne@orange.fr; j.gascoigne@bangor.ac.uk

L. Berec
Department of Theoretical Ecology, Biology Centre ASCR,
Institute of Entomology, Branišovská 31, 37005 Ceske
Budejovice, Czech Republic

S. Gregory · F. Courchamp
Ecologie, Systématique and Evolution, UMR CNRS 8079,
Université Paris-Sud, Bâtiment 362, 91405 Orsay Cedex, France

Keywords Component Allee effect ·
Demographic Allee effect · Positive density dependence ·
Mate search

Introduction

Ever since Stephens et al. (1999) coined the terms, it has been traditional to start a review paper on Allee effects

with the definition of ‘demographic’ versus ‘component’ Allee effects. It is likely that by now the interested reader will be familiar with the concepts, but to be safe, and with apologies for the repetition, we have nonetheless decided to start this review in the standard way. A ‘component Allee effect’ is a positive relationship between a given fitness component (e.g., number of matings, number of seeds produced, survival of pups to 1 year, etc.) and population size or density. A ‘demographic Allee effect’ is a positive relationship between mean overall fitness and population size or density, leading to a positive relationship between the per capita population growth rate and population size or density (Stephens et al. 1999). Component Allee effects are of interest from the point of view of understanding the ecology of a particular species, but from a broader ecological and particularly a conservation perspective, it is demographic Allee effects which are of most concern, since they have the potential to lead to catastrophic population collapse and to prevent or slow recovery from low density and population establishment or re-establishment.

One of the most intuitive and best-understood mechanisms for generating a component Allee effect is mate-finding. Indeed, so intuitive is this mechanism that, as Stephens et al. (1999) highlight, many authors use it as their definition of an Allee effect. It is easy to understand that when populations are at a reduced density, individuals may face difficulties in finding a mate. It follows that this should have an impact on some component of their reproductive fitness. There have been several modelling studies which consider the process of mate searching and demonstrate how it is related to population density (Philip 1957; Dennis 1989; McCarthy 1997; Berec et al. 2001; see also Courchamp et al. 2008 for a concise review). Although based on different assumptions concerning the subtleties of the actual mating process, all these models imply that fertilisation is more likely if more males are present, either in terms of absolute numbers or relative to the number or density of females.

Mate-finding Allee effects can be more subtle than a straightforward issue of mate search at reduced density. Individuals may need to mate several times to maximise their reproductive output. This means that, in low density populations, females may receive some matings, but not enough to fertilise all the eggs they have available. Males may likewise not be able to fulfil their full reproductive potential, even if they mate. Furthermore, in many populations, one or both sexes exercise mate choice. At low population density, mate choice may be more limited, and individuals therefore may have to settle for lower quality mates than in higher density populations. Unlike the straightforward search issue, these issues—lack of multiple matings and poor mate

quality—may also arise in dense populations, if they are relatively small.

Mate-finding can also be a passive process, for example in broadcast spawners or in plant pollination. In this case, rather than a requirement for males and females to meet, there is a requirement for male and female gametes to meet—but functionally this is also ‘mate-finding’, albeit in a broader sense. There are further subtleties—for instance in situations where the sex ratio is very skewed—which we also consider below.

Such component Allee effects are of interest in themselves, but it is also important to try and follow the link, if any, from component effects to population dynamics. If some proportion of individuals in a population are not mated, or not mated to their full potential, there may well be demographic consequences—fewer offspring per individual is likely to lead to a decline in the per capita population growth rate. However, if individuals lose out on matings which they would otherwise gain at the expense of other individuals (e.g., a reduction in the harem size of alpha males), the demographic consequences may be negligible or even positive (e.g., a genetic consequence such as an increase in the effective population size). Furthermore, it is possible that under-performance in one fitness component is offset by over-performance in another. For example, individuals at low density may obtain fewer matings but more resources. If the strength of mate-finding Allee effects varies temporally and/or spatially, individuals unable to find mates may reallocate resources from reproduction to growth, thereby improving mating success later on. We discuss various examples of such trade-offs below. Overall, for various reasons, component mate-finding Allee effects may not translate to demographic Allee effects and population processes in a straightforward way.

Mate-finding Allee effects are also of significant interest from the genetic and evolutionary perspective. There are many striking evolutionary adaptations which may have arisen in whole or in part to avoid mate-finding Allee effects—or at least more broadly to enhance individual ability to find an appropriate mate over the range of densities experienced by the population. These may include bird song, pheromones, reproductive aggregations and many others. We suggest that these adaptations can be usefully divided into two groups: (1) adaptations that mitigate the effect of low density (such as bird song and pheromones), and (2) adaptations that avoid low density altogether (such as reproductive aggregations). After reviewing the mechanisms for mate-finding Allee effects and their demographic consequences, we consider the circumstances under which these different adaptations arose, and their consequences under the impact of anthropogenic activity.

Mate-finding Allee effects

Searching for and attracting mates

This type of straightforward ‘mate-finding’—individual animals moving around to find one another for purposes of mating—is probably the most well known of all types of Allee effect. The basic theory is simple and intuitive: at a reduced density, individuals will not always be able to find a suitable, receptive mate during their own receptive period, and their reproductive output will decrease accordingly.

There are a number of models that can be used to quantify the increase in mate search time or the decrease in female mating rate with decreasing population density (reviewed in Dennis 1989; Liermann and Hilborn 2001; Courchamp et al. 2008). They predict (unsurprisingly) that a mate-finding Allee effect is most likely in species which have limited dispersal ability (Philip 1957), in populations which are dispersed in space rather than aggregated (Dobson and Lyles 1989) and where individuals are only reproductive intermittently and asynchronously (Calabrese and Fagan 2004). Other than these ‘pointers’ it is difficult to predict a priori whether this mechanism will exist in a given population. Although mate-finding Allee effects might be expected to arise mainly among animals with a solitary life style, social species may also be affected. In particular, mate location or acceptance may become a problem if breeding pairs have to be formed by individuals from different (native) social groups (e.g., African wild dogs; McCreery and Robbins 2001).

Mate-finding Allee effects due to individual searching have been proposed in terrestrial species from sheep ticks to condors and marine species from zooplankton to whales. We do not have space here to list every study on the topic and every species potentially affected, and instead direct the reader to existing reviews (Dennis 1989; Fowler and Baker 1991; Sæther et al. 1996; Wells et al. 1998; Courchamp et al. 1999, 2000, 2008; Stephens and Sutherland 1999, 2000; Liermann and Hilborn 2001; Peterson and Levitan 2001; Gascoigne and Lipcius 2004a; Levitan and McGovern 2005; Berec et al. 2007).

The strongest evidence for mate-finding Allee effects can probably be found in invertebrates (although this may be confounded by the ethical or logistical constraints of experimenting on vertebrates). For example, mate-finding Allee effects are proposed in some species of copepods (Kiørboe 2006), and as the mechanism through which some pastures stay mysteriously free of sheep ticks (Milne 1950, cited in Liermann and Hilborn 2001). Mate-finding Allee effects do not necessarily require two separate sexes in the usual ‘human’ sense; the wheat pathogen *Tilletia indica* reproduces via encounters between sporidia of different

mating strains, which are less frequent at low density (Garrett and Bowden 2002). They may occur in the malaria parasite *Plasmodium* spp. within the body of mosquitoes where sexual reproduction takes place; mosquitoes sucking blood from infected humans must suck up enough male and female *Plasmodium* gametocytes for successful reproduction within the mosquito (Pichon et al. 2000).

Studies of Allee effects, mate-finding and otherwise, have frequently focussed on invasive species (see review by Taylor and Hastings 2005). A compelling example of a component Allee effect in mate-finding, leading to a demographic Allee effect, can be found in the invasive gypsy moth (*Lymantria dispar*) in North America. In a field experiment, where pheromone traps (which attract male moths) were placed next to tethered female moths, gypsy moth were found to have a positive relationship between the probability of a female being mated and the density of males, as measured by the number of moths in the traps (Tcheslavskaja et al. 2002; Fig. 1).

Some of the most striking elements of animal behaviour are adaptations for attracting mates, including, for example, calls and song, displays, odour and pheromone marking and reproductive aggregations. A mate-finding Allee effect may arise if these mate-finding behaviours are themselves disrupted at low density. For example, heavy fishing on spawning aggregations of reef fish results in the loss of knowledge of spawning sites and migration routes from the population, as well as disruption of spawning behaviour via the removal of dominant males (Sadovy 2001). Similarly, the loss of older, more knowledgeable matriarchs is believed to result in reduced per capita reproductive success among the remaining members of

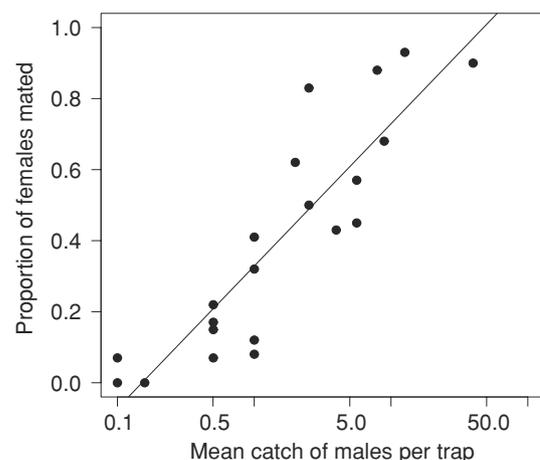


Fig. 1 A higher population density of gypsy moths (*Lymantria dispar*) (as measured by the number of males caught in pheromone traps over a given time period) resulted in a higher proportion of tethered female moths being mated; at low population densities, few females were mated, suggesting a mate-finding Allee effect (Tcheslavskaja et al. 2002)

African elephant groups (McComb et al. 2001). In neither of these cases, however, have Allee effects been specifically demonstrated. The disruption of mating aggregations through exploitation and its implications are also discussed from a more general perspective in Rowe and Hutchings (2003).

It is clear from models (e.g., Philip 1957; Berec and Boukal 2004) that dispersal or movement rates are key to creating (or avoiding) mate-finding Allee effects. Although small populations of Roesel's bush cricket (*Metrioptera roeseli*) have a smaller probability of persistence compared to larger populations (Berggren 2001), an increase in movement rates within low density populations can effectively counteract mate-finding Allee effects (Kindvall et al. 1998). If, however, individuals are more likely to disperse away from small or low density populations in search of mates (or more generally in search of a higher fitness habitat), this can exacerbate the Allee effect by reducing the per capita population growth rate of these populations still further. In the Glanville fritillary butterfly (*Melitaea cinxia*; an endangered species of northern European dry meadows), a higher proportion of males emigrate out of small populations in search of mates, and a lower proportion of females are thus mated (Kuussaari et al. 1998; Fig. 2).

Dispersal of gametes

Sessile organisms live permanently attached to land or seabed—plants are an obvious example but many animals are also sessile during reproductive maturity; notably many marine invertebrates. Others are not obligately sessile but nonetheless move around very little; this includes most

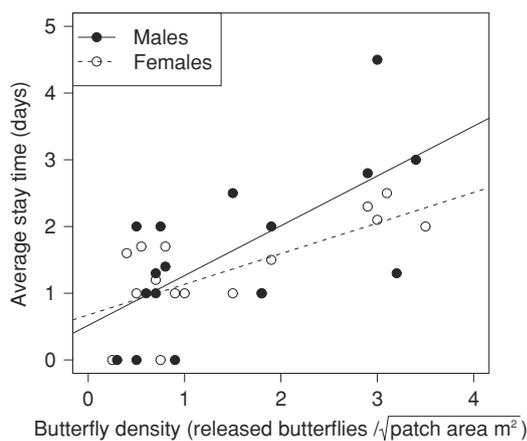


Fig. 2 Movement of newly emerged Glanville fritillaries (*Melitaea cinxia*) in relation to population density. Both male and female butterflies released in smaller groups had a higher tendency to emigrate out of the patch in search of mating opportunities (Kuussaari et al. 1998)

bivalves and echinoderms and many polychaete worms, as well as others. This mode of life requires individuals to reproduce without coming into direct contact with conspecifics. They therefore have to rely on gametes encountering a suitable 'mate' while travelling through the surrounding medium (whether water or air).

In essence, this 'mate-finding' (or gamete-finding) Allee effect arises out of the physics of diffusion, which dictates that the further the gamete cloud from an individual travels, the more dilute it becomes. It thus follows that individuals in sparse populations are likely to encounter fewer gametes from other individuals, making fertilisation less efficient and potentially causing a problem for sexual reproduction at low density. Most work on this type of Allee effect has been done on plants, but there are also some seminal studies of Allee effects of this type in broadcast spawning invertebrates, mainly echinoderms (see reviews in Levitan and McGovern 2005 and Courchamp et al. 2008, among others).

In both plants and invertebrates, fertilisation efficiency has frequently been found to be positively related to population density. A series of studies demonstrating this relationship are summarised in Figs. 3 and 4. Note that in Fig. 3 the x -axis is an (inverse) function of population

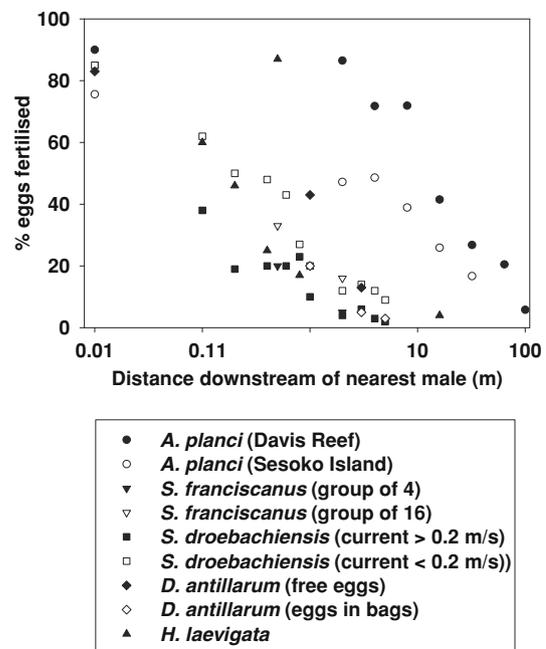


Fig. 3 Fertilisation efficiency in broadcast spawning invertebrates (four echinoderms, one gastropod), showing a general trend of exponential decline in the proportion of eggs fertilised with increasing nearest neighbour distance. Data from Babcock et al. (1994) (crown of thorns starfish, *Acanthaster planci*); Levitan et al. (1992) (red sea urchin, *Strongylocentrotus franciscanus*); Pennington (1985) (green sea urchin, *S. droebachiensis*); Levitan (1991) (Caribbean long-spined sea urchin, *D. antillarum*); Babcock and Keesing (1999) (greenlip abalone, *Haliotis laevigata*)

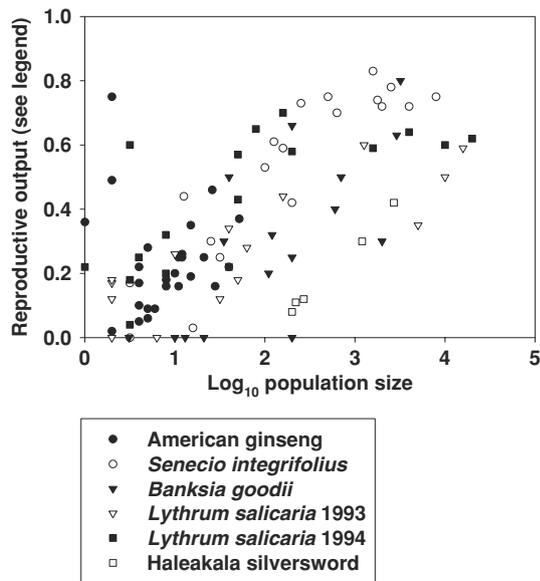


Fig. 4 Reproductive output of flowering plants as a function of population size. American ginseng (*Panax quinquefolius*): green fruits per flower versus number of individuals flowering (Hackney and McGraw 2001); *Senecio integrifolius*: proportion of seeds set versus number of individuals flowering (Widen 1993); *Banksia goodii*: proportion of plants fertile versus population size in m^3 (Lamont et al. 1993); *Lythrum salicaria*: seeds per flower/100 versus number of individuals flowering (Agren 1996); *Haleakala silversword* (*Argyroxiphium sandwicense macrocephalum*): proportion of seeds set versus number of individuals flowering synchronously (Forsyth 2003)

density (nearest-neighbour distance), while in Fig. 4 it is a function of population size. This reflects the fact that most work on pollen limitation in plants has been done on plants pollinated by some animal vector (usually insects). These actively seek out flowers, complicating the issue of dilution by diffusion. Instead, pollen limitation in these plants is driven by the fact that most pollinators move relatively short distances and are less likely to find, visit and spend time in a small or isolated patch relative to a large or interconnected patch (Sih and Baltus 1987; Wilcock and Neiland 2002; Ashman et al. 2004). Also, a generalist pollinator (the majority) will visit plants of other species—and a higher proportion of these when the species of interest is at low density. Thus, individuals in low density populations receive both less pollen and a lower proportion of conspecific pollen than those in dense populations (Ashman et al. 2004; Wagenius 2006).

Wind pollination is more directly analogous to broadcast spawning and pollen limitation is hypothesised to be very common in wind-pollinated species (Wilcock and Neiland 2002). For example, pollen limitation has been recorded in invasive annual cordgrass (*Spartina alterniflora*) where small, isolated patches of clones at the leading edge of an invasion set little seed (Davis et al. 2004). In European

beech (*Fagus sylvatica*) trees in smaller habitat patches set less seed (Nilsson and Wastljung 1987), and seed set in the blue oak (*Quercus douglasii*) may also be limited by the number of neighbours in a ~ 60 -m radius (Knapp et al. 2001). Indeed, pollen limitation may drive the mass synchronous seed set characteristic of wind-pollinated masting species (Koenig and Ashley 2003). We must not assume, however, that high seed set in larger populations is always a consequence of pollination. In the pale swallow-wort (*Vincetoxicum rossicum*; an invasive vine) larger populations had higher seed set as a consequence of the suppression of other plant species, and hence reduced interspecific competition in large patches (Cappuccino 2004). This is of course still an Allee effect, but with a different mechanism unrelated to mate-finding in any sense.

One additional complication encountered by some out-crossing plant species is the issue of self-incompatibility. Self-incompatible plant species cannot cross with individuals that possess the same self-incompatibility or S-alleles meaning that populations of self-incompatible species should have a reduced number of potential mates. On the balance of probability, fewer mating types are likely to be represented in a small population than in a large one, and therefore the likelihood of a mate-finding Allee effect is enhanced in populations with self-incompatibility. For example, plants of native perennial herb *Burchardia umbellata* set less seed following experimental selfing compared to out-crossing (Ramsey and Vaughton 2000) as was the case for experimental populations of the known invasive wild radish (*Raphanus sativus*) (Elam et al. 2007). In an extreme case, an Illinois population of the self-incompatible Lakeside daisy (*Hymenoxys acaulis*) is considered functionally extinct because the last individuals are all of the same mating type (Demauro 1993).

Sperm limitation

Sperm limitation may often arise in sessile or broadcast spawning organisms as described above. However, in mobile organisms, it is generally a question of mate-finding. However, it is not enough for a female just to find a mate: in order to maximise her reproductive output, she must find enough mates, or a large enough mate, to provide enough compatible sperm to fertilise all her eggs. In populations reduced in size or density, this may not always be possible.

Evidence for sperm limitation in natural populations of mobile species is somewhat limited. Studies have mainly focused on exploited populations, and must be treated with caution as examples of Allee effects because sperm limitation may arise due to the exploitation itself, as well as due to reduced population size, e.g., as when the fishery targets

large males. Females in heavily exploited populations of blue crab (*Callinectes sapidus*), Caribbean spiny lobster (*Panulirus argus*) and New Zealand rock lobster (*Jasus edwardsii*), for example, are frequently sperm-limited because fisheries have reduced the abundance of large males, reducing mate choice and reproductive output of individual females (MacDiarmid and Butler 1999; Hines et al. 2003; Carver et al. 2005). The distinction between sperm limitation due to low density and sperm limitation due to lack of mate choice (lack of large males) would become important if the fishery were to be stopped, because in the former case the rate of recovery of the population would be low (an Allee effect), while in the latter case it would be rapid once enough of the small males had grown to become large males. In practice, however, it is probably very difficult to distinguish the two effects in the field.

Physiological stimulation

In some species, individuals who do not encounter enough conspecifics do not become reproductive, not directly because they cannot find a mate, but rather because they need the presence of conspecifics to come into physiological condition to reproduce. This kind of physiological facilitation has been observed in captive populations, for example lemurs and flamingoes (Stevens and Pickett 1994; Hearn et al. 1996; Studer-Thiersch 2000). Presumably, the evolutionary purpose for this is to avoid wasting resources on gamete production if populations are too sparse for reproduction (i.e., if a mate-finding Allee effect is present). The specific mechanism may vary; individuals may require stimuli through exposure to conspecifics, potential mates, courtship or mating behaviour or perhaps some other related factor—in most cases the precise mechanism is unknown.

Such effects may be significant in some groups of insects. One of W.C. Allee's best-known experiments, in laboratory populations of the flour beetle (*Tribolium confusum*), showed that a dome-shaped relationship between per capita reproductive rate and density arise because the beetles need to encounter a certain density of conspecifics or mates to come into reproductive condition (Allee 1941; Allee et al. 1949). Mated queen European honey bees (*Apis mellifera*) produce structurally different pheromones to unmated queen bees, to which drones respond with increased attention and matings (Richard et al. 2007). Female golden egg bugs (*Phyllomorpha laciniata*) housed among conspecifics can lay twice as many eggs as isolated females (Garcia-Gonzalez and Gomendio 2003; Miettinen et al. 2006).

Reproductive facilitation may also be important in queen and milk conch (*Strombus gigas* and *S. costatus*),

large gastropods native to the sub-tropical western Atlantic and Caribbean. Queen conch have been heavily exploited throughout their range and, in Bermuda and Florida, populations have crashed and are showing limited signs of recovery (Berg and Olsen 1989). A survey of extensive deep-water populations of queen conch showed that there was no reproductive activity below a critical density of ~50 animals per ha (Stoner and Ray-Culp 2000). Furthermore, a translocation experiment in shallow-water populations also suggested an Allee effect (Gascoigne and Lipcius 2004b). This may be a straightforward problem of mate-finding, but reproductive facilitation may occur, because conch females engaged in egg-laying are subsequently eight times more likely to copulate than those not laying eggs (Appeldoorn 1988). Abalone (*Haliotis* spp.) is another large gastropod that may require reproductive stimulation by conspecifics. Abalones are broadcast spawners, but increase fertilisation rates by aggregating to spawn. As density declines, a decreasing proportion of reproductive adults participate in reproductive aggregations, reducing per capita reproductive output (Shepherd and Brown 1993). Multiple matings also has benefits in guppies (*Poecilia reticulata*) which produce bigger broods of fitter young (Evans and Magurran 2000), and in two-spotted crickets (*Gryllus bimaculatus*) where eggs from females mated several times have greater hatching success (Tregenza and Wedell 1998).

Animals which can reproduce asexually may nevertheless have higher reproductive output in the presence of other individuals (Thomas and Benjamin 1973). In self-fertile snails, *Biomphalaria glabrata*, and parthenogenetic female lizards, *Cnemidophorus uniparens*, individuals housed in isolation produce fewer offspring than individuals housed in groups, apparently because of exposure to courtship behaviour, although they do not actually mate (Crews et al. 1986; Vernon 1995). It is not clear what effect this might have in nature (if any), but it is interesting and counter-intuitive that even species which are self-fertile have the potential to suffer from reproductive Allee effects, particularly since self-fertilisation itself may be an evolutionary adaptation to avoid Allee effects—this is discussed further below.

Female choice and reproductive investment

Sexual selection—selection pressure on various characteristics via mate choice—plays an important role in the ecology as well as the evolution of many species. Mate choice is usually (not always) exercised by females and can take various forms, depending on the benefits which females accrue from mating with more attractive males—these benefits can be direct (male parental care) or indirect (more genetically fit or attractive male offspring) (Møller

and Thornhill 1998). In small or low-density populations where females cannot choose between males, or where choice is limited to males which are not particularly attractive, or where available males are kin, females may choose not to mate, or may invest less in reproduction and offspring, leading to lower reproductive success (Møller and Legendre 2001; Lehmann and Perrin 2003; Kokko and Mappes 2005; but see Kokko and Rankin 2006 for alternative outcomes). In mathematical models, this scenario can lead to a demographic Allee effect (Møller and Legendre 2001), but its importance in nature is less clear, although it may be one of the causes for difficulties with captive breeding programmes (Møller and Legendre 2001).

Mate-finding and demographic stochasticity

The link between demographic stochasticity and Allee effects, and more specifically whether demographic stochasticity should be considered an Allee effect mechanism, has exercised ecologists a fair amount over the last few years (Lande 1993, 1998; Stephens et al. 1999; Engen et al. 2003; Bessa-Gomes et al. 2004). Certainly, it acts mainly in small populations and increases the risk of extinction, so to that extent it looks and smells like an Allee effect. In our view, however, demographic stochasticity cannot be considered an Allee effect mechanism by itself, but it can act to create a mechanism if it has an impact on mate-finding at low density.

This becomes clear if we consider the distinction between two types of demographic stochasticity currently recognised by population ecologists: (1) random fluctuations in population size resulting from individual birth and death events, and (2) random fluctuations in the adult sex ratio in populations with two sexes. Random fluctuations in birth and death rates do not fit our Allee effect definition because individual fitness, or a component of individual fitness, is not affected in a density-dependent way. Instead, chance events drive individuals out of the population or allow them to reproduce with a probability that is density-independent. A sequence of detrimental chance events may drive the entire population to extinction, and this is obviously more likely when there are fewer individuals: as a result, the probability that the population size collapses increases as the population declines. However, because Allee effects concern individual fitness, demographic stochasticity in births and deaths cannot in our view be classified as an Allee effect mechanism, even though it increases extinction risk in small populations (Stephens et al. 1999; Bessa-Gomes et al. 2004).

On the other hand, sex ratio fluctuations arguably do reduce mean individual fitness as the population declines, via the mechanism of mate-finding. They arise both as a consequence of chance in determining offspring sex, and

because of demographic stochasticity in male and female deaths which, even if the male and female death rates are equal, causes the male-to-female ratio to vary unpredictably. As the population size increases, the adult sex ratio is less and less likely to deviate from 1:1 so that nearly every individual within the population will be able to find a mate. Because demographic stochasticity due to random fluctuations in the adult sex ratio reduces a component of individual fitness, via mate-finding as the population declines, it can be reasonably considered an Allee effect mechanism (Stephens et al. 1999; Bessa-Gomes et al. 2004). This kind of Allee effect is more likely to occur in monogamous than polygynous populations (Engen et al. 2003; Bessa-Gomes et al. 2004), and has been modelled in marmots (Stephens et al. 2002) and measured in small plant populations (Soldaat et al. 1997), although in neither case were individual fitness or per capita population growth rate measured directly. Another case, widely advertised at the time, is the kakapo (*Strigops habroptilus*), a lek-breeding giant, flightless parrot native to New Zealand. In 2001, the world population of this flightless bird consisted of 54 individuals, of which only 21 were female (with only a few of these being fertile), distributed across several islands. An intensive breeding program has resulted in the birth of several chicks, but only six female fledglings have been produced since 1982 (Elliott et al. 2001; Sutherland 2002). The smaller the breeding population, the more likely are random fluctuations in the adult sex ratio to lead to a dramatically male-biased population, with little possibility of recovery.

From mate-finding to demographic Allee effects

As mentioned in the introduction, the connection from component Allee effects via mate-finding to demographic Allee effects is not always clear. Nonetheless, there are convincing examples of demographic Allee effects which arise from mate-finding. These currently include the Glanville fritillary, the gypsy moth, the smooth cordgrass and a copepod *Hesperodiptomus shoshone* (Table 1). In addition, Table 1 lists those species we know of in which evidence for the link between a mate-finding Allee effect and a demographic Allee effect is somewhat weaker, often mediated by population models, and those studies in which the link is promising yet remains speculative.

A productive approach in linking component with demographic Allee effects has been to combine field data with population modelling. This cannot, of course, give a definitive causal connection between population size and per capita population growth rate, but it can nonetheless be highly instructive. For example, in an invasive population of the wind-pollinated grass *Spartina alterniflora*,

Table 1 Studies where an evidence for a demographic Allee effect was brought up and a link to a mate-finding Allee effect either demonstrated or suggested

Species	Mechanism	Evidence	Human impacts?	Refs
<i>Strong evidence for the link between a mate-finding Allee effect and a demographic Allee effect</i>				
Smooth cordgrass <i>Spartina alterniflora</i>	Pollination failure demonstrated	Reduced (but still positive) per capita population growth rate at low density in front of invasion	Yes; invasive species	Davis et al. (2004); Taylor et al. (2004)
Gypsy moth, <i>Lymantria dispar</i>	Mate-finding limitation demonstrated	Threshold size below which colony goes extinct	Yes; introduced species	Tcheslavskaja et al. (2002); Liebhold and Bascombe (2003)
Glanville fritillary, <i>Melitaea cinxia</i>	Mate-finding limitation demonstrated	Hump-shaped relationship between per capita population growth rate and population size	Yes; habitat loss and fragmentation	Kuussaari et al. (1998)
Copepod, <i>Hesperodiaptomus shoshone</i>	Mate-finding limitation demonstrated	Failure of populations to establish in experimental lakes with initial copepod densities <3 individuals/m ³	Yes; fish stocking reduced original populations	Samelle and Knapp (2004); Kramer et al. (2008)
<i>Weak evidence for the link between a mate-finding Allee effect and a demographic Allee effect</i>				
<i>Gentianella campestris</i>	Pollination failure demonstrated	Models suggest threshold in extinction probability in non-selfing populations	Yes; extinction and reintroduction	Lennartsson (2002)
House finch, <i>Carpodacus mexicanus</i>	Mate-finding limitation demonstrated	Modelling suggests Allee effect due to mate-finding in early stages of establishment	Yes; introduced species	Veit and Lewis (1996)
<i>Likely but speculative evidence for the link between a mate-finding Allee effect and a demographic Allee effect</i>				
Various parasitoids	Mate-finding limitation leading to skewed sex ratios suggested	Persistence of populations positively related to propagule numbers released size or number of releases	Yes; biocontrol species	Hopper and Roush (1993)
Queen conch, <i>Strombus gigas</i>	Reproductive failure possible; predation may be more important	~100% mortality of juveniles away from aggregation; reduced reproduction at low density; collapse and failure to recover from overfishing in many areas	Yes; heavy fishing pressure	Berg and Olsen (1989); Stoner and Ray (1993); Ray and Stoner (1994)
Atlantic cod, <i>Gadus morhua</i>	Mate-finding limitation demonstrated, cultivation effect suggested	Per capita population growth rate ~ zero in population reduced by overfishing	Yes; overfishing	Swain and Sinclair (2000); Walters and Kitchell (2001); Rowe et al. (2004)
Elk, <i>Cervus elaphus nelsoni</i>	Mate-finding possible; acclimatisation may be more important	Higher % breeding in years following introduction than in the year of introduction	Yes; reintroduction programme	Larkin et al. (2002)
<i>Banksia goodii</i>	Pollination failure possible	Reproductive failure of smallest populations	Yes; habitat loss and fragmentation	Lamont et al. (1993)
<i>Clarkia concinna</i>	Pollination failure possible	Reproductive failure of smallest populations if isolated	No	Groom (1998)

We somewhat subjectively classify these cases into three categories according to the perceived degree of confidence in the link, as strong, weak or speculative

population models suggested that pollen limitation in sparsely populated areas would reduce the per capita population growth rate, although it still remained positive at all sites (a ‘weak’ demographic Allee effect; Davis et al. 2004; Taylor et al. 2004). The same approach was used on reintroduced populations of the field gentian (*Gentianella campestris*), a herb of rare low-nutrient grasslands (Lennartsson 2002). Some individuals of *G. campestris* are self-fertile while others are not, and the trait is heritable. Non-selfing populations showed a threshold patch size below which seed set fell dramatically, and demographic models suggested that these populations had high extinction probabilities. In self-compatible populations, no such critical thresholds were predicted. A mate-finding (pollen-limitation) Allee effect may thus be a driver for the evolution of self-fertile strains within some species (see the next section). This approach is equally applicable to animals and can be used with great success to understand the dynamics of biological invasions. Using independent estimates of life-history parameters, Veit and Lewis (1996) constructed a model that closely mirrored the observed dynamics of the invasion of the house finch (*Carpodacus mexicanus*) in North America, including a 3- to 10-year lag from its initial introduction to the first recorded instances of breeding that they speculated was caused by a mate-finding Allee effect.

There are, however, many studies that demonstrate mate-finding Allee effects but do not attempt to demonstrate ensuing demographic Allee effects, and vice versa. The majority of studies that consider mate-finding at low density consider processes at an individual rather than a population level (i.e., component rather than demographic Allee effects). Studies which have attempted to uncover empirical evidence of demographic Allee effects (e.g., Myers et al. 1995; Sæther et al. 1996; Liermann and Hilborn 1997; Sibly et al. 2005) have not found much empirical support. This failure to detect demographic Allee effects may be simply because overall fitness and per capita population growth rate are both very difficult to measure in the field, as well as because of methodological biases which make it more difficult to detect positive than negative density dependence (reviewed in Courchamp et al. 2008, Ch. 5). However, component mate-finding Allee effects may be disconnected from demographics for more substantive reasons. In particular, two main issues arise which may mitigate the effect of a component Allee effect at the population level: fitness trade-offs and spatial structure in populations or metapopulations.

Fitness trade-offs occur when different components of fitness have different density-dependent relationships. For example, reproductive output may be positively related to density via mate-finding, but other fitness components may be negatively density-dependent. In the island fox

(*Urocyon littoralis*), for example, low density results in a lower proportion of mated females, but eventually leads to more pups per female since (presumably) more resources are available to each female (Angulo et al. 2007). In this case, however, the effect of multiple component Allee effects tipped the cost-to-benefit balance of low density towards the cost side, and a demographic Allee effect was observed.

These trade-offs are also well illustrated by examples from plant pollination and broadcast spawners. Plants that have high rates of seed set (i.e., close to 100% fertilisation efficiency) can suffer reduced growth and reproduction the following year. This cost associated with high seed set can mean that populations with low fertilisation efficiency have a similar overall mean population growth rate to populations with high fertilisation efficiency (Ehrlen 1992; Ehrlen and Eriksson 1995). Pollen limitation could also in theory trade off with reduced intraspecific competition at low density, but we have not come across a study which has addressed this hypothesis in plants. In sea urchins, however, this hypothesis has been tested. Echinoderms can pull off a variety of neat physiological tricks, including the ability to shrink their body mass when times get hard (Levitan 1991). Individuals in sparse populations are thus generally larger, because competition for resources is lower. In the Caribbean long-spined sea urchin (*Diadema antillarum*), increased gamete production by larger individuals at low density seems to offset the reduction in fertilisation efficiency, so that individual reproductive output remains broadly similar across a wide range of densities (Levitan 1991). If population density, and thus Allee effects, fluctuate significantly in time and space, individuals unable to find mates may reallocate resources from current reproduction to future growth which may improve mating success in subsequent seasons, as observed, for example, in the pipefish (*Syngnathus typhle*) (Berglund 1991).

The other confounding issue in converting mate-finding component Allee effects into demographic consequences is population spatial structure. Populations or sub-populations which are connected to their neighbours via dispersal can be brought back from below the Allee threshold by immigration from nearby patches (the ‘rescue’ effect). The two significant factors which determine whether the chance of extinction due to a demographic Allee effect will be mitigated via immigration are (1) the isolation of the (sub-) population and (2) the cost of dispersal across the intervening matrix. This is not the place to enter a discussion of Allee effects and metapopulation dynamics (see reviews in Amarasekare 1998 and Courchamp et al. 2008), but it is interesting to note the important role that population isolation often plays when demographic Allee effects are detected in populations with component mate-finding Allee effects.

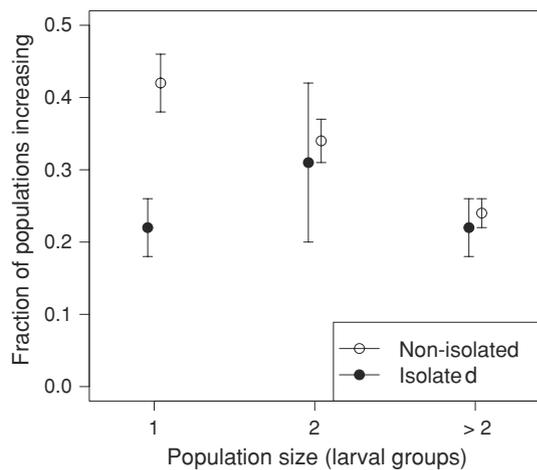


Fig. 5 The mate-finding Allee effect in the Glanville fritillary shown in Fig. 2 leads to a demographic Allee effect in the isolated populations, whereby population growth rate is depressed at low population size. In non-isolated populations, there is no such Allee effect

As an example, we return to the Glanville fritillary, which has a component Allee effect in mate-finding, illustrated in Fig. 5. This component Allee effect was shown in this case to lead to a demographic Allee effect in isolated populations, with a dome-shaped relationship between per capita population growth rate (measured as the proportion of populations increasing versus decreasing, as with the gypsy moth) and population size. In non-isolated populations, there was no demographic Allee effect (Kuussaari et al. 1998; Fig. 5). The role of isolation in converting component mate-finding Allee effects into demographic Allee effects has also been illustrated in studies of plants (Groom 1998) and echinoderms (Levitan 2002a).

Measuring demographic Allee effects directly usually requires very extensive datasets. On the one hand, we may attempt to detect a demographic Allee effect in a single population monitored over consecutive years. While this approach has been attempted on a number of occasions (e.g., Myers et al. 1995; Sæther et al. 1996; Liermann and Hilborn 1997; Walters and Kitchell 2001; Barrowman et al. 2003; Reed 2005; Sibly et al. 2005), none have revealed extensive evidence for demographic Allee effects and all have, at least in part, suggested that this might be due to data constraints. On the other hand, we may attempt to measure a demographic Allee effect with replicate populations—quite a rarity particularly for species of interest to conservation biologists, but there are exceptions. In their island fox study, Angulo et al. (2007) used populations on different islands in an archipelago as replicates. In the gypsy moth, an extensive network of 150,000 pheromone traps across the northeastern USA has provided a very large data set which can be analysed to look at trends in

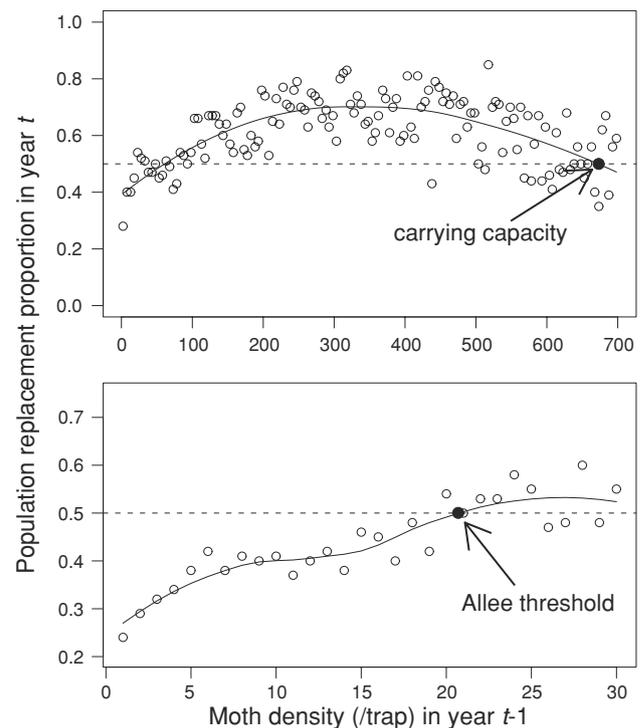


Fig. 6 The proportional size P of the population in year t (y-axis) relative to the population size in year $t - 1$ (x-axis). The Allee threshold at $P = 0.5$ works out at ~ 20.7 moths per trap, the carrying capacity at ~ 673 moths per trap. The *bottom panel* is a close-up of the low-density populations of the *top one*. Redrawn from Tobin et al. (2007)

population dynamics in relation to population density (Johnson et al. 2006; Tobin et al. 2007).

Tobin et al. (2007) used a subset of this trap data to calculate for each integer value of population size the proportion P of populations which increased from 1 year to the next. At the Allee threshold, $P = 0.5$ because a population at the threshold size is equally likely to increase or decrease the following year. They found an Allee threshold, with smaller populations more likely to decrease because of a failure to find mates (Tcheslavskaja et al. 2002), while larger populations were more likely to increase (Fig. 6). (There is also a higher density threshold at which $P = 0.5$, this corresponds to the carrying capacity.)

Intriguingly, the Allee threshold in the gypsy moth is not consistent in space or time, with a lower Allee threshold in Wisconsin than Virginia and a lower threshold in 2002–2003 than 2003–2004. The geographical variation in the threshold was strongly correlated with geographical variation in the invasion rate (Whitmire and Tobin 2006; Tobin et al. 2007) in line with general model predictions (e.g., Almeida et al. 2006). It may be that the effectiveness of mate-finding (pheromone transmission) varies depending on the environment in a similar way to pollination with an

animal vector (Wilcock and Neiland 2002), although Tcheslavskaja et al. (2002) speculate that predation may play an important role. Also, it appears that the optimal environment for gypsy moths at high densities is not necessarily the best at low densities—Virginia and North Carolina had a higher Allee threshold than Wisconsin (i.e., provided a less good environment for low density populations) but also had an estimated carrying capacity more than twice as high (i.e., provided a better environment for high density populations; Tobin et al. 2007).

Evolution to mitigate or avoid mate-finding Allee effects: consequences for depleted populations

In this review, we also consider mate-finding Allee effects from an evolutionary point of view. Since an Allee effect is, by definition, a process that affects individual fitness, it is subject to natural selection. We therefore ask whether the risk of suffering from mate-finding Allee effects might have been a significant evolutionary driver for different mate-finding adaptations and even mating systems.

Adaptations for finding a mate—and finding the best mate—are very widespread, ranging from sex or aggregation pheromones to bird songs, to ability to move faster or more efficiently, to pollination mutualisms, to mass spawning and to quality advertising through honest signals. We believe it is useful to distinguish between mechanisms which allow mate-finding at low density (e.g., long-distance attractants such as calling and pheromones) and adaptations which reduce the likelihood of low density per se (e.g., mass spawning or reproductive aggregations). This is because, from a theoretical perspective, the consequences of these two types of adaptations in terms of Allee effects are different. If the mate-finding mechanism has evolved to function well even at low density, it seems likely that the population will not be particularly vulnerable to Allee effects at low density. If, however, the mate-finding mechanism has evolved to ensure that low density is avoided, it seems to us reasonable to hypothesise that this population will be vulnerable to mate-finding Allee effects should it ever meet with low density. Thus, although gregariousness can still be an adaptation to mitigate or avoid a mate-finding Allee effect, the Allee effect is still there and is only circumvented by avoiding low density. Both types of adaptation may thus have a similar purpose, but in the context of populations reduced by anthropogenic impacts their effects can be diametrically opposed. Species with the former types of adaptation are less likely to suffer from mate-finding Allee effects, since they are already adapted to cope with low density. Conversely, species with the latter type may suffer very severely if their populations are artificially reduced to low

density, since their mating system is predicated precisely on avoiding low density. Paradoxically, therefore, species which have adapted mechanisms to circumvent mate-finding Allee effects may now be precisely those which find themselves most vulnerable. The fourth column in Table 1, which indicates whether there has been an anthropogenic impact on the populations in question, suggests that this “evolutionary” classification of mate-finding adaptations might have merit.

Modelling studies suggest that mate-finding adaptations can indeed mitigate mate-finding Allee effects. For example, Jonsson et al. (2003) compared the efficiency of a pheromone and a non-pheromone mate-finding strategy at different conspecific densities. Whereas there were only small differences between these strategies at high density, the pheromone strategy was more efficient when conspecific density declined. With another simulation model, Berec et al. (2001) showed that mate-finding Allee effects can be avoided either by a large number of individuals with relatively low mate-finding ability or a few individuals with high mate-finding ability—an increase in the mate detection distance significantly decreased strength of the mate-finding Allee effect.

In reality, it is not usually possible to say whether a particular evolutionary adaptation arose specifically because of a mate-finding Allee effect. For example, bird songs or amphibian advertisement calls apparently help individuals increase their probability of mating if they are dispersed and potentially difficult to locate, such as in the Cuban tree frog (*Osteopilus septentrionalis*; Vargas-Salinas 2006). However, such signals may also serve as a tool in intense intra-sexual competition in male-biased breeding aggregations—indeed, call duration was shown to be an indicator of genetic quality in males of the grey tree frog (*Hyla versicolor*; Welch et al. 1998). In such instances, it is possible that the signal originated in sparse populations so as to facilitate mate-finding (you are chosen because you are audible), before it became exaggerated and used for sexual selection (you are chosen because you are louder than your competitors). However, it is also possible that it originated in large populations for exactly the same reason: to increase the chance that you are noticed by a female earlier than your mute competitors. Thus, any adaptation likely to arise as a response to mate-finding Allee effects in rare populations should be scrutinised from the perspective of its origin. Below, we consider some of the adaptations that allow mate-finding at low density and therefore might arise as a response to mate-finding Allee effects in rare populations.

Traits that have only a negligible adaptive value in large and dense populations might turn out to be strong determinants of fitness when populations become small and sparse, i.e., during population bottlenecks. The case of

biological invasions is a particularly significant example of this. During the early founding of an invading population, these populations may be exposed to situations that are very different from normal conditions and thus for which they may not be pre-adapted. Specifically, founding populations differ from established populations in that not only are they at very low densities but they are also extremely isolated spatially from other populations. This can promote a diversification of mate-finding traits between invading and source populations, a situation that would not be experienced in continuously established populations.

Mate encounters in animals

Behaviourally plastic strategies which mitigate mate-finding Allee effects have been observed in Roesel's bush cricket (*Metrioptera roeseli*) (faster movement at low population densities; Kindvall et al. 1998) and the European field cricket (*Gryllus campestris*) (higher proportion of males calling at low population densities; Hissmann 1990). Some adaptations decrease the frequency at which mate-finding needs to occur. Such adaptations may be highly advantageous at low density, but may be of little benefit at high density. They include the ability of females to store viable sperm (e.g., the box turtle, *Terrapene carolina*; Ewing 1943, and many invertebrates), induced ovulation (e.g., the red deer, *Cervus elaphus*; Jabbour et al. 1994), and ability to maintain long-term or even life-long pair bonds (e.g., the wandering albatross, *Diomedea exulans*; Dubois et al. 1998: in migrating species, such as the albatross, this works together with breeding site fidelity—another adaptation—allowing them to find each other in the breeding season). The ability of females to store sperm is important in many marine species, particularly in crustaceans where mating usually has to coincide with moulting and therefore where only short mate-finding windows are available. In the blue crab, females only mate once, during their terminal moult, and store sperm which is used for the rest of their reproductive life (up to several years) (Carver et al. 2005).

Adaptations to mitigate or avoid mate-finding Allee effects might also involve shifts in mating systems. Mating systems as diverse as parthenogenesis, hermaphroditism, arrhenotoky, or even density-dependent sex determination, all help individuals in mating in low-density populations. Parthenogenesis requires no mate-finding at all, and can be permanent, such as in some whiptail lizards (*Cnemidophorus* sp.; Cole 1984), or only seasonal such as in various nematodes, rotifers, (parasitic) wasps, mites or aphids. Simultaneous (self-incompatible) hermaphrodites such as hamlets (coral reef fish, *Hypoplectrus* spp.) effectively double the density of mating partners relative to species with separate sexes, since any two individuals can in

principle mate. Some hermaphrodites, such as tapeworms and perhaps some molluscs, may even evolve selfing when mate availability is limited (Klomp et al. 1964). Sometimes, the shift in reproductive strategy may impact female reproductive behaviour. Hopper and Roush (1993) showed that a change from virgin females producing no progeny (sexual reproduction with diploid sex determination) to virgin females producing all males (arrhenotoky; sexual reproduction with haplo-diploid sex determination) decreased the critical number of females needed for population persistence by over 30%. In some cases, introduced species which were biparental in their native ranges appear to have become parthenogenetic in their introduced ranges where finding mates becomes difficult (Hopper and Roush 1993 and references therein). Copepodites (juvenile stage) of the parasitic copepod *Pachypygus gibber* (Becheikh et al. 1998) or sexually undifferentiated larvae of the echinuran worm *Bonellia viridis* (Berec et al. 2005 and references therein) become males or females (in part) depending on availability of sexual partners.

Pollen limitation in plants

From the above, it is clear that low density or rarity may induce shifts in animal mating systems towards cloning or selfing. A similar shift may also occur in plants. However, the genetic costs associated with high selfing rates (i.e., inbreeding depression) may mean that populations of rare plants suffer two opposing Allee effects, one related to inbreeding where self-pollination dominates and the other to mate-finding where self-pollination is prohibited. Where inbreeding depression strongly reduces individual fitness, evolution may 'prefer' inbreeding avoidance and lead to a self-incompatibility system, dioecy or heterostyly. On the other hand, where inbreeding depression is weak, rare populations of outcrossing plants may avoid mate-finding Allee effects by evolving self-pollination (Lloyd 1992; Herlihy and Eckert 2002). In the California annual *Clarkia xantiana*, for example, small populations isolated from congeners exhibited reduced herkogamy and protandry (traits promoting self-fertilisation avoidance) relative to large populations or small populations mingled with congeners (Moeller and Geber 2005). Outcrossing is ancestral in *C. xantiana* and self-pollination has likely evolved in small or sparse populations living in inferior, arid habitats and hence suffering lower pollinator visitation rates (Moore and Lewis 1965; Fausto et al. 2001).

Modelling studies support these predictions. Cheptou (2004) and Morgan et al. (2005) showed that natural selection might lead plants to evolve either complete selfing in which case an Allee effect due to pollen limitation disappears, or complete non-selfing with a strong Allee

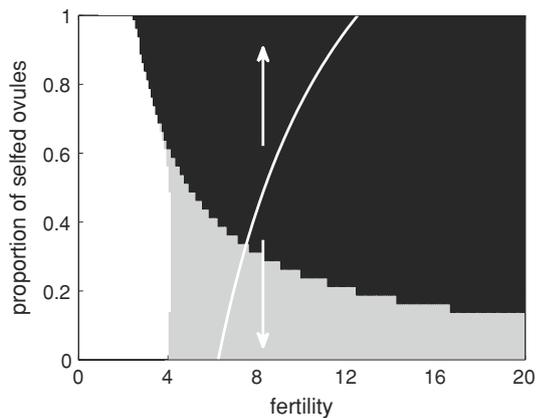


Fig. 7 An outcome of a model examining the evolution of selfing as a function of fertility and initial proportion of selfed ovules. The plant population suffers from effect with an Allee threshold in the *grey* area and a weak or no demographic Allee effect in the *black* area; the population goes extinct from any initial size in the *white* area. The *white* curve delimits the area in which plants evolve complete selfing (above the curve) from the area where they evolve complete non-selfing (below the curve); the *arrows* demonstrate the route of evolution. Adapted from Cheptou (2004)

effect due to pollen-limitation (Fig. 7). The evolutionary endpoint depends on a variety of population characteristics, such as the strength of inbreeding depression, the strength of pollen-limitation Allee effect, fertility, and the initial state of partial selfing. At least in theory, selection for selfing may even lead to population extinction, a phenomenon termed ‘evolutionary suicide’ (Cheptou 2004; Morgan et al. 2005). Such models usually consider inbreeding depression to be constant (i.e., not specified by an underlying population genetic model nor dependent on population size or density). This assumption may not be robust enough and implies that more detailed models should be developed and analysed. This new generation of models might also shed some light on the idea that the (often) intermediate selfing rates seen in nature could be viewed as a trade-off between maximising fertilisation (mate-finding) on the one hand and avoiding inbreeding depression on the other—trying to avoid two kinds of Allee effects simultaneously.

Rare plants may also mitigate pollen-limitation Allee effects by evolving higher pollinator attraction (Haig and Westoby 1988), allocating more resources to clonal growth (Eckert 2002) or ‘sacrificing’ dioecy for simultaneous hermaphroditism (Wilson and Harder 2003; see also Ashman et al. 2004 for a comprehensive review). Many sparse plant species have succeeded in avoiding both pollen limitation and inbreeding, by evolving highly specific mutualisms between one plant species and one species of pollinator (often insects, but also bats: Sakai 2002; Jackson 2004; Maia and Schlindwein 2006; Muchhala 2006).

Broadcast spawning in marine invertebrates

Adaptations that mitigate Allee effects via reduced fertilisation success at low density in broadcast spawning marine invertebrates are reviewed by Levitan (1998). These include spawning synchrony (using cues such as day length, lunar period or phytoplankton concentration), increased mobility and aggregation, sperm filtering and storage, hermaphroditism and selfing.

A nice comparison of three congeneric sea urchins shows how sperm limitation may stimulate the evolution of gamete morphology and performance (Levitan 2002b). The urchin *Strongylocentrotus droebachiensis* living habitually at the lowest density has evolved gametes that perform best under sperm limitation (larger eggs and slow, long-lived sperm). On the other hand, the urchin *S. purpuratus* that lives at the highest density has evolved gametes that perform best under sperm competition (smaller eggs and fast, short-lived sperm). *Strongylocentrotus franciscanus* lives at an intermediate density and its gametes have intermediate traits. These observations suggest that gametes of *S. purpuratus* would perform suboptimally when density of this species is abruptly reduced, since any mutation of the egg or sperm in the direction of *S. droebachiensis* would be advantageous and quickly spread through the population, and vice versa. Interestingly, *S. droebachiensis*, evolving a fertilisation system with higher success rates at low sperm concentrations than the other two urchins, bears a cost in the form of higher rates of hybridisation with the other species at high (total) sperm density (Levitan 2002a).

A word of caution

One can think of many adaptations that might have been selected in small or sparse populations as an evolutionary response to mate-finding Allee effects. On the other hand, as exemplified by the evolution of sexual reproduction, large or dense populations might have acquired traits that generate Allee effects and thus impose costs only as the population declines. Many of the above ideas and considerations are only suggestive, not conclusive. However appealing these may be, only a careful examination of the advantages of an evolutionary strategy among a sea of other strategies may help us to assess the extent to which the observed adaptations have evolved as a response to mate-finding Allee effects. As we already cautioned above; some adaptations that may appear to be a result of natural selection in small or sparse populations may equally be seen as outcomes of sexual selection acting in large or dense populations.

In our opinion, convincing evidence of evolution to mitigate or avoid Allee effects needs to show that a trait value increasing fitness at low density has a cost associated with it at high density. This is not to say that such a trait

must necessarily have a cost at high density, but rather that if we found such an example it would be the most convincing evidence that evolution had occurred to avoid some cost associated with low density (as in the example of *S. droebachiensis* above). Mathematical models of evolution, such as those considering competitive dynamics between initially small populations of mutants and large populations of resident phenotypes, could also help discriminate from among many possible evolutionary outcomes. It is notable that, although there are many population dynamical models involving Allee effects, relatively few models have been developed that consider how individuals respond evolutionarily to mate-finding (or other) Allee effects.

The amazingly rich world of mating systems and mate-finding adaptations, some of which may have evolved as a response to mate-finding Allee effects, leads us to wonder whether there is any chance of observing demographic Allee effects at all, or whether these adaptations, the ‘ghosts of Allee effects past’, are all we can expect to see in natural populations. Given this possibility, we suggest that it would be most productive to look for demographic Allee effects in populations which are ‘anthropogenically’ rather than ‘naturally’ rare (i.e., populations reduced greatly in size due to habitat loss, exploitation, etc., or non-native populations at the start of an invasion). This is because such populations (although they are now small or sparse) may have an evolutionary history of being large or dense. This means that they have not experienced the conditions over evolutionary time which would result in selective pressure to mitigate the negative impacts of low density (i.e., of Allee effects). It is thus these populations that we would expect to be most vulnerable to demographic Allee effects when they are reduced by human activity. Again, a brief glance at Table 1 suggests that this hypothesis has merit, since all but one presented example of demographic Allee effects demonstrated or suggested to be driven by mate-finding are in populations affected by human activity.

Conclusions

In this paper, we have reviewed just one of the many possible mechanisms giving rise to component Allee effects—mate-finding—and done so with numerous examples. We have also discussed populations which show compelling evidence of demographic Allee effects arising from mate-finding; however, there are significantly fewer examples of these in the scientific literature at the moment (we have found four). Given the huge number of populations of sexually reproducing species that could, according to the arguments we present above, suffer from mate-finding component Allee effects, not to mention all the

other populations that may be susceptible to other Allee effect mechanisms, we might ask why there are so few empirical examples of ensuing demographic Allee effects. If component Allee effects were widespread and potent enough to drive evolutionary selection of adaptations to avoid them, as argued above, we should be able to detect more demographic Allee effects, particularly in populations which are threatened, endangered or otherwise reduced in number or density, of which there are (alas) many examples (see <http://www.iucnredlist.org/>).

We believe that the lack of hard experimental evidence for the effects of mate-finding Allee effects on demography results from the difficulties of studying field populations at small sizes or low densities. Indeed, there are real difficulties associated with the empirical investigation of Allee effects in natural populations. These include, among other things, the need for a long time-series or a wide spectrum of densities, technical problems associated with statistical analysis, non-independence and replication, issues around the definition of a population, and of population spatial structure and metapopulation dynamics, and logistical problems in working in the field—issues with which many readers will no doubt be all too familiar (see review in Courchamp et al. 2008). Studies which do provide convincing demonstrations of demographic Allee effects have often studied rather exceptional systems (e.g., many replicate populations of different densities in a wide geographical area; Johnson et al. 2006). As a matter of fact, only a small number of studies demonstrating mate-finding Allee effects undertook a way of demonstrating presence or absence of a demographic Allee effect.

Negative density dependence is now considered by most to be a real population regulatory phenomenon (Berryman 2002), to the extent that some have argued that it should be considered a ‘principle’ of population ecology (Berryman 2003). This is at least in part due to the strength of empirical evidence for negative density dependence dynamics in natural populations (e.g., Brook and Bradshaw 2006). It has also been argued that positive density dependence, or Allee dynamics, should also be upgraded to the status of a ‘principle’ (Berryman 2003). It is easy to put forward theoretical reasons why Allee dynamics could be considered a ‘principle’ of population ecology; however, with the presently limited empirical evidence we struggle to support such claims convincingly.

The visible importance of adaptations for mate-finding implies that mate-finding Allee effects may have been an important source of selection pressure on populations in the past. Given our role in reducing many populations to small size or low density, it seems likely that they may continue to be so. In our view, and in the view of others (Brook 2008), we need to work hard to surmount the obstacles associated with studying Allee effects at the population level, or find

imaginative means of circumventing them, if we are ever to have convincing evidence that demographic Allee effects are of general importance in population dynamics, whether as a consequence of mate-finding or of some other mechanism, and that they are (or are not) as widespread as we suspect.

Acknowledgments J.G. acknowledges financial support from BBSRC, as well as the continued support of the School of Ocean Sciences, University of Wales Bangor. L.B. acknowledges financial support from the Grant Agency of the Academy of Sciences of the Czech Republic (KJB600070602) and from the Institute of Entomology (Z50070508), S.G. and F.C. benefitted from a grant by the Agence Nationale de la Recherche.

References

- Agren J (1996) Population size, pollinator limitation and seed set in the self-incompatible herb *Lythrum salicaria*. *Ecology* 77:1779–1790. doi:10.2307/2265783
- Allee WC (1941) Animal aggregations, a study in general sociology. University of Chicago Press, Chicago
- Allee WC, Emerson O, Park T, Schmidt K (1949) Principles of animal ecology. Saunders, Philadelphia
- Almeida RC, Delphim SA, da S. Costa MI (2006) A numerical model to solve single species invasion problems with Allee effects. *Ecol Modell* 192:601–617. doi:10.1016/j.ecolmodel.2005.07.018
- Amarasekare P (1998) Allee effects in metapopulation dynamics. *Am Nat* 152:298–302. doi:10.1086/286169
- Angulo E, Roemer GW, Berec L, Gascoigne J, Courchamp F (2007) Double Allee effects and extinction in the island fox. *Conserv Biol* 21:1082–1091. doi:10.1111/j.1523-1739.2007.00721.x
- Appeldoorn RS (1988) Fishing pressure and reproductive potential in strombid conchs: is there a critical stock density for reproduction? *Mem Soc Cienc Nat La Salle* 48:275–288
- Ashman TL, Knight TM, Steets JA, Amarasekare P, Burd M, Campbell DR, Dudash MR, Johnston MO, Mazer SJ, Mitchell RJ, Morgan MT, Wilson WG (2004) Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. *Ecology* 85:2408–2421. doi:10.1890/03-8024
- Babcock R, Keesing J (1999) Fertilisation biology of the abalone *Haliotis laevis*: laboratory and field studies. *Can J Fish Aquat Sci* 56:1668–1678. doi:10.1139/cjfas-56-9-1668
- Babcock RC, Mundy CN, Whitehead D (1994) Sperm diffusion models and in situ confirmation of long-distance fertilization in the free-spawning asteroid *Acanthaster planci*. *Biol Bull* 186:17–28. doi:10.2307/1542033
- Barrowman NJ, Myers RA, Hilborn R, Kehler DG, Field CA (2003) The variability among populations of coho salmon in the maximum reproductive rate and depensation. *Ecol Appl* 13:784–793. doi:10.1890/1051-0761(2003)013[0784:TVAPOC]2.0.CO;2
- Becheikh S, Michaud M, Thomas F, Raibaut A, Renaud F (1998) Roles of resource and partner availability in sex determination in a parasitic copepod. *Proc R Soc Lond B* 265:1153–1156. doi:10.1098/rspb.1998.0411
- Berec L, Boukal DS (2004) Implications of mate search, mate choice and divorce rate for population dynamics of sexually reproducing species. *Oikos* 104:122–132. doi:10.1111/j.0030-1299.2004.12753.x
- Berec L, Boukal DS, Berec M (2001) Linking the Allee effect, sexual reproduction, and temperature-dependent sex determination via spatial dynamics. *Am Nat* 157:217–230. doi:10.1086/318626
- Berec L, Schembri PJ, Boukal DS (2005) Sex determination in *Bonellia viridis* (Echiura: Bonelliidae): population dynamics and evolution. *Oikos* 108:473–484. doi:10.1111/j.0030-1299.2005.13350.x
- Berec L, Angulo E, Courchamp F (2007) Multiple Allee effects and population management. *Trends Ecol Evol* 22:185–191. doi:10.1016/j.tree.2006.12.002
- Berg CJ, Olsen D (1989) Conservation and management of queen conch (*Strombus gigas*) fisheries in the Caribbean. In: Caddy JF (ed) Marine invertebrate fisheries: their assessment and management. Wiley, New York
- Berggren A (2001) Colonization success in Roesel's bush-cricket *Metrioptera roeseli*: the effects of propagule size. *Ecology* 82:274–280
- Berglund A (1991) Egg competition in a sex-role reversed pipefish—subdominant females trade reproduction for growth. *Evol Int J Org Evol* 45:770–774. doi:10.2307/2409928
- Berryman AA (2002) Population regulation, emergent properties, and a requiem for density dependence. *Oikos* 99:600–606. doi:10.1034/j.1600-0706.2002.12106.x
- Berryman AA (2003) On principles, laws and theory in population ecology. *Oikos* 103:695–701. doi:10.1034/j.1600-0706.2003.12810.x
- Bessa-Gomes C, Legendre S, Clobert J (2004) Allee effects, mating systems and the extinction risk in populations with two sexes. *Ecol Lett* 7:802–812. doi:10.1111/j.1461-0248.2004.00632.x
- Brook B (2008) The allure of the few. *PLoS Biol* 6:e127. doi:10.1371/journal.pbio.0060127
- Brook BW, Bradshaw CJA (2006) Strength of evidence for density dependence in abundance time series of 1198 species. *Ecology* 87:1445–1451. doi:10.1890/0012-9658(2006)87[1445:SOEFDD]2.0.CO;2
- Calabrese JM, Fagan WF (2004) Lost in time, lonely, and single: reproductive asynchrony and the Allee effect. *Am Nat* 164:25–37. doi:10.1086/421443
- Cappuccino N (2004) Allee effect in an invasive alien plant, pale swallow-wort *Vincetoxicum rossicum* (Asclepiadaceae). *Oikos* 106:3–8. doi:10.1111/j.0030-1299.2004.12863.x
- Carver AM, Wolcott TG, Wolcott DL, Hines AH (2005) Unnatural selection: effects of a male focused size-selective fishery on reproductive potential of a blue crab population. *J Exp Mar Biol Ecol* 319:29–41. doi:10.1016/j.jembe.2004.06.013
- Cheptou PO (2004) Allee effect and self-fertilization in hermaphrodites: reproductive assurance in demographically stable populations. *Evol Int J Org Evol* 58:2613–2621
- Cole CJ (1984) Unisexual lizards. *Sci Am* 250:94–100
- Courchamp F, Clutton Brock T, Grenfell B (1999) Inverse density dependence and the Allee effect. *Trends Ecol Evol* 14:405–410. doi:10.1016/S0169-5347(99)01683-3
- Courchamp F, Clutton Brock T, Grenfell B (2000) Multipack dynamics and the Allee effect in the African wild dog, *Lycaon pictus*. *Anim Conserv* 3:277–285. doi:10.1111/j.1469-1795.2000.tb00113.x
- Courchamp F, Berec L, Gascoigne J (2008) Allee effects in ecology and conservation. Oxford University Press, Oxford
- Crews D, Grassman M, Lindzey J (1986) Behavioral facilitation of reproduction in sexual and unisexual Whiptail lizards. *Proc Natl Acad Sci USA* 83:9547–9550. doi:10.1073/pnas.83.24.9547
- Davis HG, Taylor CM, Lambrinos JG, Strong DR (2004) Pollen limitation causes an Allee effect in a wind-pollinated invasive grass (*Spartina alterniflora*). *Proc Natl Acad Sci USA* 101:13804–13807. doi:10.1073/pnas.0405230101
- Demauro MM (1993) Relationship of breeding system to rarity in the Lakeside Daisy (*Hymenoxys acaulis* var *glabra*). *Conserv Biol* 7:542–550. doi:10.1046/j.1523-1739.1993.07030542.x
- Dennis B (1989) Allee effects: population growth, critical density and the chance of extinction. *Nat Resour Model* 3:481–538

- Dobson AP, Lyles AM (1989) The population-dynamics and conservation of primate populations. *Conserv Biol* 3:362–380. doi:10.1111/j.1523-1739.1989.tb00242.x
- Dubois F, Cezilly F, Pagel M (1998) Mate fidelity and coloniality in waterbirds: a comparative analysis. *Oecologia* 116:433–440. doi:10.1007/s004420050607
- Eckert CG (2002) The loss of sex in clonal plants. *Evol Ecol* 15:501–520. doi:10.1023/A:1016005519651
- Ehrlen J (1992) Proximate limits to seed production in a herbaceous perennial legume, *Lathyrus-vernus*. *Ecology* 73:1820–1831. doi:10.2307/1940033
- Ehrlen J, Eriksson O (1995) Pollen limitation and population-growth in a herbaceous perennial legume. *Ecology* 76:652–656. doi:10.2307/1941223
- Elam DR, Ridley CE, Goodell K, Ellstrandt NC (2007) Population size and relatedness affect fitness of a self-incompatible invasive plant. *Proc Natl Acad Sci USA* 104:549–552. doi:10.1073/pnas.0607306104
- Elliott GP, Merton DV, Jansen PW (2001) Intensive management of a critically endangered species: the kakapo. *Biol Conserv* 99:121–133. doi:10.1016/S0006-3207(00)00191-9
- Engen S, Lande R, Sæther BE (2003) Demographic stochasticity and Allee effects in populations' with two sexes. *Ecology* 84:2378–2386. doi:10.1890/02-0123
- Evans JP, Magurran AE (2000) Multiple benefits of multiple mating in guppies. *Proc Natl Acad Sci USA* 97:10074–10076. doi:10.1073/pnas.180207297
- Ewing H (1943) Continued fertility in female Box turtles following mating. *Copeia* 1943:112–114. doi:10.2307/1437776
- Fausto JA, Eckhart VM, Geber MA (2001) Reproductive assurance and the evolutionary ecology of self-pollination in *Clarkia xantiana* (Onagraceae). *Am J Bot* 88:1794–1800. doi:10.2307/3558355
- Forsyth S (2003) Density-dependent seed set in the Haleakala silversword: evidence for an Allee effect. *Oecologia* 136:551–557. doi:10.1007/s00442-003-1295-3
- Fowler C, Baker J (1991) A review of animal population dynamics at extremely reduced population levels. *Rep Int Whaling Comm* 41:545–554
- Garcia-Gonzalez F, Gomendio M (2003) Oviposition site selection and oviposition stimulation by conspecifics in the golden egg bug (*Phyllomorpha laciniata*): implications for female fitness. *Behav Ecol Sociobiol* 53:385–392
- Garrett KA, Bowden RL (2002) An Allee effect reduces the invasive potential of *Tilletia indica*. *Phytopathology* 92:1152–1159. doi:10.1094/PHYTO.2002.92.11.1152
- Gascoigne J, Lipcius RN (2004a) Allee effects in marine systems. *Mar Ecol Prog Ser* 269:49–59. doi:10.3354/meps269049
- Gascoigne J, Lipcius RN (2004b) Conserving populations at low abundance: delayed functional maturity and Allee effects in reproductive behaviour of the queen conch *Strombus gigas*. *Mar Ecol Prog Ser* 284:185–194. doi:10.3354/meps284185
- Groom MJ (1998) Allee effects limit population viability of an annual plant. *Am Nat* 151:487–496. doi:10.1086/286135
- Hackney EE, McGraw JB (2001) Experimental demonstration of an Allee effect in American ginseng. *Conserv Biol* 15:129–136. doi:10.1046/j.1523-1739.2001.98546.x
- Haig D, Westoby M (1988) On limits to seed production. *Am Nat* 131:757–759. doi:10.1086/284817
- Hearn GW, Berghaier RW, George DD (1996) Evidence for social enhancement of reproduction in two *Eulemur* species. *Zoo Biol* 15:1–12. doi:10.1002/(SICI)1098-2361(1996)15:1<1::AID-ZOO1>3.0.CO;2-F
- Herlihy CR, Eckert CG (2002) Genetic cost of reproductive assurance in a self-fertilizing plant. *Nature* 416:320–323. doi:10.1038/416320a
- Hines AH, Jivoff PR, Bushmann PJ, van Montfrans J, Reed SA, Wolcott DL, Wolcott TG (2003) Evidence for sperm limitation in the blue crab, *Callinectes sapidus*. *Bull Mar Sci* 72:287–310
- Hissmann K (1990) Strategies of mate finding in the European field cricket (*Gryllus campestris*) at different population-densities—a field-study. *Ecol Entomol* 15:281–291. doi:10.1111/j.1365-2311.1990.tb00810.x
- Hopper KR, Roush RT (1993) Mate finding, dispersal, number released, and the success of biological-control introductions. *Ecol Entomol* 18:321–331. doi:10.1111/j.1365-2311.1993.tb01108.x
- Jabbour HN, Veldhuizen FA, Mulley RC, Asher GW (1994) Effect of exogenous gonadotropins on estrus, the Lh surge and the timing and rate of ovulation in red deer (*Cervus-elaphus*). *J Reprod Fertil* 100:533–539. doi:10.1530/jrf.0.1000533
- Jackson AP (2004) Cophylogeny of the *Ficus microcosm*. *Biol Rev Camb Philos Soc* 79:751–768. doi:10.1017/S1464793104006463
- Johnson DM, Liebhold AM, Tobin PC, Bjornstad ON (2006) Allee effects and pulsed invasion by the gypsy moth. *Nature* 444:361–363. doi:10.1038/nature05242
- Jonsson M, Kindvall O, Jonsell M, Nordlander G (2003) Modelling mating success of saproxylic beetles in relation to search behaviour, population density and substrate abundance. *Anim Behav* 65:1069–1076. doi:10.1006/anbe.2003.2141
- Kindvall O, Vessby K, Berggren A, Hartman G (1998) Individual mobility prevents an Allee effect in sparse populations of the bush cricket *Metrioptera roeseli*: an experimental study. *Oikos* 81:449–457. doi:10.2307/3546766
- Kjørboe T (2006) Sex, sex-ratios, and the dynamics of pelagic copepod populations. *Oecologia* 148:40–50. doi:10.1007/s00442-005-0346-3
- Klomp H, van Monfort MAJ, Tammes PML (1964) Sexual reproduction and underpopulation. *Arch Neerl Zool* 16:105–110
- Knapp EE, Goedde MA, Rice KJ (2001) Pollen-limited reproduction in blue oak: implications for wind pollination in fragmented populations. *Oecologia* 128:48–55. doi:10.1007/s004420000623
- Koenig WD, Ashley MV (2003) Is pollen limited? The answer is blowin' in the wind. *Trends Ecol Evol* 18:157–159. doi:10.1016/S0169-5347(03)00034-X
- Kokko H, Mappes J (2005) Sexual selection when fertilization is not guaranteed. *Evol Int J Org Evol* 59:1876–1885
- Kokko H, Rankin DJ (2006) Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Philos Trans R Soc Lond B* 361:319–334
- Kramer A, Sarmelle O, Knapp RA (2008) Allee effect limits colonization success of sexually reproducing zooplankton. *Ecology* 89:2760–2769
- Kuussaari M, Saccheri I, Camara M, Hanski I (1998) Allee effect and population dynamics in the Glanville fritillary butterfly. *Oikos* 82:384–392. doi:10.2307/3546980
- Lamont BB, Klinkhamer PGL, Witkowski ETF (1993) Population fragmentation may reduce fertility to zero in *Banksia-goodii*—a demonstration of the Allee effect. *Oecologia* 94:446–450. doi:10.1007/BF00317122
- Lande R (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *Am Nat* 142:911–927. doi:10.1086/285580
- Lande R (1998) Demographic stochasticity and Allee effect on a scale with isotropic noise. *Oikos* 83:353–358. doi:10.2307/3546849
- Larkin JL, Maehr DS, Cox JJ, Wichrowski MW, Crank RD (2002) Factors affecting reproduction and population growth in a restored elk *Cervus elaphus nelsoni* population. *Wildl Biol* 8:49–54
- Lehmann L, Perrin N (2003) Inbreeding avoidance through kin recognition: choosy female boost male dispersal. *Am Nat* 162:638–652. doi:10.1086/378823

- Lennartsson T (2002) Extinction thresholds and disrupted plant–pollinator interactions in fragmented plant populations. *Ecology* 83:3060–3072
- Levitan DR (1991) Influence of body size and population-density on fertilization success and reproductive output in a free-spawning invertebrate. *Biol Bull* 181:261–268. doi:10.2307/1542097
- Levitan DR (1998) Sperm limitation, sperm competition and sexual selection in external fertilizers. In: Birkhead TR, Møller AP (eds) Sperm competition and sexual selection. Academic Press, Burlington, pp 173–215
- Levitan DR (2002a) The relationship between conspecific fertilization success and reproductive isolation among three congeneric sea urchins. *Evol Int J Org Evol* 56:1599–1609
- Levitan DR (2002b) Density-dependent selection on gamete traits in three congeneric sea urchins. *Ecology* 83:464–479
- Levitan DR, McGovern T (2005) The Allee effect in the sea. In: Norse E, Crowder L (eds) Marine conservation biology: the science of maintaining the sea's biodiversity. Island Press, Washington DC, pp 47–57
- Levitan DR, Sewell MA, Chia FS (1992) How distribution and abundance influence fertilisation success in the sea urchin *Strongylocentrotus franciscanus*. *Ecology* 73:248–254. doi:10.2307/1938736
- Liebold A, Bascombe J (2003) The Allee effect, stochastic dynamics and the eradication of alien species. *Ecol Lett* 6:133–140. doi:10.1046/j.1461-0248.2003.00405.x
- Liermann M, Hilborn R (1997) Depensation in fish stocks: a hierarchic Bayesian meta-analysis. *Can J Fish Aquat Sci* 54:1976–1984. doi:10.1139/cjfas-54-9-1976
- Liermann M, Hilborn R (2001) Depensation: evidence, models and implications. *Fish Fish* 2:33–58. doi:10.1046/j.1467-2979.2001.00029.x
- Lloyd DG (1992) Self-fertilization and cross-fertilization in plants. 2. The selection of self fertilization. *Int J Plant Sci* 153:370–380. doi:10.1086/297041
- MacDiarmid AB, Butler MJ (1999) Sperm economy and limitation in spiny lobsters. *Behav Ecol Sociobiol* 46:14–24. doi:10.1007/s002650050587
- Maia ACD, Schlindwein C (2006) *Caladium bicolor* (Araceae) and *Cyclocephata celata* (Coleoptera, Dynastinae): a well-established pollination system in the northern Atlantic rainforest of Pernambuco, Brazil. *Plant Biol* 8:529–534. doi:10.1055/s-2006-924045
- McCarthy MA (1997) The Allee effect, finding mates and theoretical models. *Ecol Modell* 103:99–102. doi:10.1016/S0304-3800(97)00104-X
- McComb K, Moss C, Durant SM, Baker L, Sayialel S (2001) Matriarchs as repositories of social knowledge in African elephants. *Science* 292:491–494. doi:10.1126/science.1057895
- McCreery EK, Robbins RL (2001) Proximate explanations for failed pack formation in *Lycaon pictus*. *Behaviour* 138:1467–1479. doi:10.1163/156853901317367708
- Miettinen M, Kaitala A, Smith RL, Ordóñez RM (2006) Do egg carrying and protracted copulation affect mobility in the golden egg bug? *J Insect Behav* 19:171–178. doi:10.1007/s10905-006-9015-6
- Moeller DA, Geber MA (2005) Ecological context of the evolution of self-pollination in *Clarkia xantiana*: population size, plant communities, and reproductive assurance. *Evol Int J Org Evol* 59:786–799
- Møller AP, Legendre S (2001) Allee effect, sexual selection and demographic stochasticity. *Oikos* 92:27–34. doi:10.1034/j.1600-0706.2001.920104.x
- Møller AP, Thornhill R (1998) Male parental care, differential parental investment by females and sexual selection. *Anim Behav* 55:1507–1515. doi:10.1006/anbe.1998.0731
- Moore DM, Lewis H (1965) The evolution of self-pollination in *Clarkia xantiana*. *Evol Int J Org Evol* 19:104–114. doi:10.2307/2406299
- Morgan MT, Wilson WG, Knight TM (2005) Plant population dynamics, pollinator foraging, and the selection of self-fertilization. *Am Nat* 166:169–183. doi:10.1086/431317
- Muchhala N (2006) Nectar bat stows huge tongue in its rib cage. *Nature* 444:701–702. doi:10.1038/444701a
- Myers RA, Barrowman NJ, Hutchings JA, Rosenburg AA (1995) Population-dynamics of exploited fish stocks at low population-levels. *Science* 269:1106–1108. doi:10.1126/science.269.5227.1106
- Nilsson SG, Wastljung U (1987) Seed predation and cross-pollination in mast-seeding beech (*Fagus sylvatica*) patches. *Ecology* 68:260–265. doi:10.2307/1939256
- Pennington JT (1985) The ecology of fertilization of echinoid eggs: the consequences of sperm dilution, adult aggregation, and synchronous spawning. *Biol Bull* 169:417–430. doi:10.2307/1541492 Woods Hole
- Peterson C, Levitan D (2001) The Allee effect: a barrier to recovery by exploited species. In: Reynolds JD, Mace GM, Redford KH, Robinson JG (eds) Conservation of exploited species. Cambridge University Press, Cambridge, pp 281–300
- Philip JR (1957) Sociality and sparse populations. *Ecology* 38:107–111. doi:10.2307/1932132
- Pichon G, Awono Ambene HP, Robert V (2000) High heterogeneity in the number of *Plasmodium falciparum* gametocytes in the bloodmeal of mosquitoes fed on the same host. *Parasitology* 121:115–120. doi:10.1017/S0031182099006277
- Ramsey M, Vaughton G (2000) Pollen quality limits seed set in *Burchardia umbellata* (Colchicaceae). *Am J Bot* 87:845–852. doi:10.2307/2656892
- Ray M, Stoner AW (1994) Experimental-analysis of growth and survivorship in a marine gastropod aggregation—balancing growth with safety in numbers. *Mar Ecol Prog Ser* 105:47–59. doi:10.3354/meps105047
- Reed DH (2005) Relationship between population size and fitness. *Conserv Biol* 19:563–568. doi:10.1111/j.1523-1739.2005.00444.x
- Richard F, Tarpy DR, Grozinger CM (2007) Effects of insemination quantity on honey bee queen physiology. *PLoS ONE* 2:e980. doi:10.1371/journal.pone.0000980
- Rowe S, Hutchings JA (2003) Mating systems and the conservation of commercially exploited marine fish. *Trends Ecol Evol* 18:567–572. doi:10.1016/j.tree.2003.09.004
- Rowe S, Hutchings JA, Bekkevold D, Rakin A (2004) Depensation, probability of fertilization, and the mating system of Atlantic cod (*Gadus morhua* L.). *ICES J Mar Sci* 61:1144–1150. doi:10.1016/j.icesjms.2004.07.007
- Sadovy Y (2001) The threat of fishing to highly fecund fishes. *J Fish Biol* 59:90–108
- Sæther BE, Ringsby TH, Roskaft E (1996) Life history variation, population processes and priorities in species conservation: towards a reunion of research paradigms. *Oikos* 77:217–226. doi:10.2307/3546060
- Sakai S (2002) A review of brood-site pollination mutualism: plants providing breeding sites for their pollinators. *J Plant Res* 115:161–168. doi:10.1007/s102650200021
- Sarnelle O, Knapp RA (2004) Zooplankton recovery after fish removal: limitations of the egg bank. *Limnol Oceanogr* 49:1382–1392
- Shepherd SA, Brown LD (1993) What is an Abalone stock—implications for the role of refugia in conservation. *Can J Fish Aquat Sci* 50:2001–2009. doi:10.1139/f93-224
- Sibly RM, Barker D, Denham MC, Hone J, Pagel M (2005) On the regulation of populations of mammals, birds, fish, and insects. *Science* 309:607–610. doi:10.1126/science.1110760

- Sih A, Baltus MS (1987) Patch size, pollinator behavior, and pollinator limitation in Catnip. *Ecology* 68:1679–1690. doi:10.2307/1939860
- Soldaat LL, Vetter B, Klotz S (1997) Sex ratio in populations of *Silene otites* in relation to vegetation cover, population size and fungal infection. *J Veg Sci* 8:697–702. doi:10.2307/3237374
- Stephens PA, Sutherland WJ (1999) Consequences of the Allee effect for behaviour, ecology and conservation. *Trends Ecol Evol* 14:401–405. doi:10.1016/S0169-5347(99)01684-5
- Stephens P, Sutherland W (2000) Vertebrate mating systems, Allee effects and conservation. In: Apollonio M, Festa-Bianchet M, Mainardi D (eds) *Vertebrate mating systems*. World Scientific Publishing, Singapore, pp 186–213
- Stephens PA, Sutherland WJ, Freckleton RP (1999) What is the Allee effect? *Oikos* 87:185–190. doi:10.2307/3547011
- Stephens PA, Frey Roos F, Arnold W, Sutherland WJ (2002) Model complexity and population predictions. The alpine marmot as a case study. *J Anim Ecol* 71:343–361. doi:10.1046/j.1365-2656.2002.00605.x
- Stevens EF, Pickett C (1994) Managing the social environments of flamingos for reproductive success. *Zoo Biol* 13:501–507. doi:10.1002/zoo.1430130512
- Stoner AW, Ray M (1993) Aggregation dynamics in juvenile Queen conch (*Strombus-gigas*)—population-structure, mortality, growth, and migration. *Mar Biol (Berl)* 116:571–582. doi:10.1007/BF00355476
- Stoner AW, Ray-Culp M (2000) Evidence for Allee effects in an over-harvested marine gastropod: density-dependent mating and egg production. *Mar Ecol Prog Ser* 202:297–302. doi:10.3354/meps202297
- Studer-Thiersch A (2000) What 19 years of observation on captive Greater flamingos suggests about adaptations to breeding under irregular conditions. *Waterbirds* 23:150–159. doi:10.2307/1522160
- Sutherland WJ (2002) Conservation biology—science, sex and the kakapo. *Nature* 419:265–266. doi:10.1038/419265a
- Swain DP, Sinclair AF (2000) Pelagic fishes and the cod recruitment dilemma in the Northwest Atlantic. *Can J Fish Aquat Sci* 57:1321–1325. doi:10.1139/cjfas-57-7-1321
- Taylor CM, Hastings A (2005) Allee effects in biological invasions. *Ecol Lett* 8:895–908. doi:10.1111/j.1461-0248.2005.00787.x
- Taylor CM, Davis HG, Cville JC, Grevstad FS, Hastings A (2004) Consequences of an Allee effect in the invasion of a pacific estuary by *Spartina alterniflora*. *Ecology* 85:3254–3266. doi:10.1890/03-0640
- Tchesslavskaja K, Brewster CC, Sharov AA (2002) Mating success of gypsy moth (Lepidoptera: Lymantriidae) females in Southern Wisconsin. *Great Lakes Entomol* 35:1–7
- Thomas J, Benjamin M (1973) The effects of population density on growth and reproduction of *Biomphalaria glabrata* (Say) (Gasteropoda: Pulmonata). *J Anim Ecol* 43:31–50. doi:10.2307/3156
- Tobin PC, Whitmire SL, Johnson DM, Bjornstad ON, Liebhold AM (2007) Invasion speed is affected by geographical variation in the strength of Allee effects. *Ecol Lett* 10:36–43. doi:10.1111/j.1461-0248.2006.00991.x
- Tregenza T, Wedell N (1998) Benefits of multiple mates in the cricket *Gryllus bimaculatus*. *Evol Int J Org Evol* 52:1726–1730. doi:10.2307/2411345
- Vargas-Salinas F (2006) Breeding behavior and colonization success of the Cuban treefrog *Osteopilus septentrionalis*. *Herpetologica* 62:398–408. doi:10.1655/0018-0831(2006)62[398:BBACSO]2.0.CO;2
- Veit RR, Lewis MA (1996) Dispersal, population growth, and the Allee effect: dynamics of the house finch invasion of eastern North America. *Am Nat* 148:255–274. doi:10.1086/285924
- Vernon JG (1995) Low reproductive output of isolated, self-fertilizing snails—introbreeding depression or absence of social facilitation. *Proc R Soc Lond B* 259:131–136. doi:10.1098/rspb.1995.0020
- Wagenius S (2006) Scale dependence of reproductive failure in fragmented *Echinacea* populations. *Ecology* 87:931–941. doi:10.1890/0012-9658(2006)87[931:SDORFI]2.0.CO;2
- Walters C, Kitchell JF (2001) Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. *Can J Fish Aquat Sci* 58:39–50. doi:10.1139/cjfas-58-1-39
- Welch AM, Semlitsch RD, Gerhardt HC (1998) Call duration as an indicator of genetic quality in male gray tree frogs. *Science* 280:1928–1930. doi:10.1126/science.280.5371.1928
- Wells H, Strauss EG, Rutter MA, Wells PH (1998) Mate location, population growth and species extinction. *Biol Conserv* 86:317–324. doi:10.1016/S0006-3207(98)00032-9
- Whitmire SL, Tobin PC (2006) Persistence of invading gypsy moth populations in the United States. *Oecologia* 147:230–237. doi:10.1007/s00442-005-0271-5
- Widen B (1993) Demographic and genetic effects on reproduction as related to population size in a rare perennial herb *Senecio integrifolius* (Asteraceae). *Biol J Linn Soc Lond* 50:179–195. doi:10.1111/j.1095-8312.1993.tb00925.x
- Wilcock C, Neiland R (2002) Pollination failure in plants: why it happens and when it matters. *Trends Plant Sci* 7:270–277. doi:10.1016/S1360-1385(02)02258-6
- Wilson WG, Harder LD (2003) Reproductive uncertainty and the relative competitiveness of simultaneous hermaphroditism versus dioecy. *Am Nat* 162:220–241. doi:10.1086/376584